

where the former cannot be employed. For coördination of series in two distant places between which there is no stratigraphical connection, paleontological evidence is the only evidence available.

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*On the Lungs of the Ophidia.*

By Prof. E. D. Cope.

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The condition of knowledge as to the characters of the lungs of snakes was stated by Stannius, in 1856,\* as follows: "The detailed accounts as to the single or double character of the lungs leave much to be desired. Among Ophidia Angiostomata there possess a single sack, Rhinophis and all Typhlopidae which have been examined; as to the Tortricidae [Ilysiidae], there are apparently species with two lungs (*T. xenopeltis*) [= *Xenopeltis unicolor*], and others with a single lung (*T. scytale*) [= *Ilysia scytale*]. Among Eurystomata, all the Peropoda (Boa, Python, Eryx) possess apparently two lungs. The Calamarina that have been investigated have one lung. Among Colubrina and Glyphodonta, there are great variations. All the Coronellæ of Schlegel possess, according to Schlegel, a single lung. I find the lung single in *Rhachiodon scaber* [*Dasypeltis*]. *Tropidonotus natrix* [*Natrix vulgaris*] has a very small rudiment of a second lung. *Coluber* [*Spilotes*] *variabilis* possesses, according to Schlegel, the rudiment of a second lung. According to the statement of Meckel, this rudiment is common in *Coluber*. The Xenodons have, according to Schlegel, a single lung (*X. severus* and *X. rhabdocephalus*). In *Heterodon* I find a rudimental second lung. The Lycodons, according to Schlegel, possess a single lung; as also do *Psammophis* and *Homalopsis*. In *Dendrophis colubrina* Schlegel found the rudiment of the second lung. In *Dipsas*, according to Schlegel, there are variations; but he states that *D. multimaculata*, *D. laevis* and *D. annulata* [*Sibon annulatum*], have but one lung. The Achrochordina have but one lung. Among Hydrophidae I found in three species of Hydrophis the lung-sack simple. Meckel states that *Platurus* has a very small rudiment of a second lung. Among the remaining poisonous snakes there is an insignificant rudiment of the second lung in the Elapina and Crotalina; while the Viperina possess an entirely simple lung."

The absence of tangible external characters which furnish indications of affinity in the Ophidia is well known. The important characters to be found in the skeleton were mostly pointed out by Müller, and Duméril and Bibron examined and utilized the characters of the dentition. The

\* *Zootomie der Amphibien*, p. 108.

characters derived from the skeleton define only the larger divisions; while those derived from the teeth are not sufficiently numerous and important, with some exceptions, to indicate all of the affinities of the genera. I think I have added materially to the means at our disposal for classifying the Ophidia, by a study of the hemipenis.\* The criteria will however not be sufficient until the entire anatomy is worked out, and in the present paper I add what may be found by a study of the lungs. It seemed probable to me that an organ which presents so much variation, as above stated by Stannius, must furnish some important clues. My examinations embraced about one hundred and fifty species, which represent nearly all the leading types. The results are presented in the following pages. It will be seen that they correct the statements of Schlegel and Stannius in a number of important respects.

The snakes with rudimental posterior limbs (Peropoda), show in the character of their lungs, what they show in the rudimental limbs themselves, and in the hemipenis, the nearest relationships to the Lacertilia. They possess, with an exception to be noted later, two well-developed lungs, one of which is larger than the other. The smaller lung lies to the right side and ventrally, while the larger one lies to the left side and dorsally. In some species the dorsal and ventral relation is more pronounced than in others. In the Colubroidea the right or ventral lung is generally present, but of very much reduced proportions, the usual size being from two to five millimeters in length. It is connected with the other lung by a foramen which perforates the tracheal cartilage at a point a little beyond the apex of the heart, and opposite to the proximal part of the dorsal lung. It is sometimes connected to the dorsal lung by a short tube, in which cartilaginous half rings are seen in but two of the genera examined, viz., *Heterodon* and *Conopsis*. The lumen of the rudimental lung may be lined by the same reticulate structure as is seen in the dorsal lung, or its walls may be smooth. In some Colubroidea the rudimental lung is absent, but such species are relatively few.

The dorsal lung may present proximally alongside of the trachea an auricle or pocket, and this is so developed in the genus *Heterodon* as to reach to the head, without communication with the trachea, other than that furnished by the normal portion of the lung. In the *Solenoglypha*, without exception, this extension of the dorsal lung is present, and extends to the head, and its lumen is continuous with the trachea throughout its length. The same structure exists in the genera *Hydrus* and *Hydrophis*; and also in the peropodous genus *Ungualia*, which differs besides from other Peropoda in having but one posttracheal lung. Finally the tracheal lung, as I shall call it, is distinct from the true lung in *Platurus* and in *Chersydrus*. In the former of these genera the trachea is not separate from the lumen; while in *Chersydrus* it is distinct. It, however, communicates with the cells of which the lung consists in this genus by a series of regularly placed foramina on each side. There is no lumen in the tracheal lung in

\* *American Naturalist*, 1893, p. 477.

Chersydrus. In Typhlops we have a still further modification of the tracheal lung. It is without lumen, and is composed of coarse cells of different sizes. These have no communication with the trachea or lung that I can discover, nor any efferent orifice. It has occurred to me that this structure, which extends from the heart to the throat, may not be a pulmonary organ.

I have referred to the dorsal and ventral positions of the two lungs. The rudimental lung is to the right of the dorsal lung in the Colubroidea, but in the Ilysiidæ it is to the left. It is quite questionable which lung this rudiment in this family really represents. In the Typhlopidae, the single lung is on the right side and extends from the heart to the liver. It has the position of the rudimental lung of the Colubroidea, and may represent it. I cannot decide this question without further material. In Glauconia there is but one true lung, and this is ventral in position, and originates to the right of the heart, so that in this genus also it may represent the rudimental lung of the Colubroidea. There is here no tracheal lung or organ.\*

I now give a synopsis of the characters observed in the species examined.

#### CATODONTA.

*Glauconia dulcis* B. and G. A single elongate right lung; no rudiment of left lung. No tracheal lung.

#### EPANODONTA.

*Typhlops liberiensis* Hallow.; *T. reticulatus* L. A right lung which is not elongate; no rudimental left lung. A cellular body surrounding the trachea, and extending from the heart to the throat, without lumen or connection with the trachea or lung.

The presence of the tracheal lung (?) and the freedom of the maxillary bone are points of resemblance to the Solenoglypha!

#### TORTRICINA.

##### *Ilysiidæ.*

Two lungs, the ventral one to the left side of the middle line, rudimental, but lined with pulmonary tissue like the other lung, and less reduced than in the Colubroidea.

*Cylindrophis maculata* L. The right lung extends only to the liver.

*Ilysia scytale* L. The right lung is larger.

##### *Rhinophidæ.*

*Rhinophis oxyrhynchus* Schn. One large left lung and very small (3 mm.) right lung; no tracheal lung. Contrary to the statement of Stannius above quoted, as in Colubroidea generally.

\* Cf. Peters, *Reise nach Mozambique*, iii, p. 100, Pl. xivA, 1882.

## ASINEA.

## PEROPODA.

I. Two well-developed lungs of unequal size ; no tracheal lung.

*Pythonidæ.*

*Python regius* Shaw ; *P. molurus* Linn. ; *P. spilotes* Lacep. ; *Loxocemus bicolor* Cope.

*Boidæ.*

*Xiphosoma caninum* L. ; *Epicrates cenchria* L. ; *Chilabothrus inornatus* Rein. ; *Boa constrictor* L. ; *Eunectes murinus* L. ; *Eryx johnii* Russ.

*Charinidæ.*

Besides the absence of coronoid and supra and postorbital bones, this family differs from the Boidæ in the fusion of the nasal bones into a single plate. *Charina bottæ* Blv.

II. One lung without rudiment of a second ; a tracheal lung extending from true lung, with which it is continuous, to throat.

*Ungaliidæ.*

*Ungalia maculata* Bibr. ; *U. melanura* Gray.

## COLUBROIDEA.

I. Two well-developed but unequal functional lungs.

*Xenopeltidæ.*

*Xenopeltis unicolor*, Reinwt.

II. One functional lung only ; the right rudimental lung sometimes possibly with limited function.

*Colubridæ.*

## Lycodontinæ.

*Lycodon aulicus* L. ; *Boaodon infernalis* Gthr. ; *Uriechis microlepidotus* Pet. ; *Stenorhina ventralis* D. and B.

## Colubrinæ.

*Elopops modestus* Gthr.\* ; *Coronella girundica* Daud. ; *Dianodon semicarinatus* Cope ; *Ficimia olivacea* Gray ; *Salvadora bairdii* Jan. ; *Pityophis sayi* Hobr. ; *Epiglottophis pleurosuctus* D. and B. ; *Spilotes corais* Cuv. ; *S. pullatus* L. ; *Coluber quadrilineatus* Pallas ; *C. obsoletus* Say ; *C. quadrivittatus* Holbr. ; *Bascanium constrictor* L. ; *B. flagellum* Catesby ; *B. mentovarium* D. and B. ; *Zamenis atrovirens* Shaw ; *Z. korros* L. ;

\* Position uncertain ; perhaps a Lycodontine.

*Cyclophis æstivus* L. ; *Drymobius pantherinus* Merr. ; *D. boddartii* Seetz. ; *D. margariferus* Schl. ; *Crossanthera melanotropis* Cope ; *Herpetodryas carinatus* L. ; *Leptophis præstans* Cope ; *L. mexicanus* D. and B. ; *L. smaragdinus* Boie. ; *Dendrophis picta* L. ; *Dasypeltis palmarum* Leach.

#### Dipsadinae.

*Dipsas blandingii* Hallow. ; *Himantodes gemmistratus* Cope ; *Rhinobothryum lentiginosum* Scop. ; *Trimorphodon biscutatus* D. and B. ; *Sibon septentrionale* Kenn. ; *Malpolon lacertinum* Wagl. ; *Cladophis kirtlandii* Hall ; *Dryophis fulgida* Daud. ; *Passerita mycterizans* L.

#### Chrysopeleinae.

*Chrysopelea ornata* Shaw.

#### Xenodontinae.

*Catostoma badium* D. and B. ; *Furancia abocura* Holbr. ; *Abastor erythrogrammus* Daud. ; *Ophionomorphus fuscus* Cope ; *Helicops angulatus* Linn. ; *H. baliogaster* Cope ; *Dromicus parvifrons* Cope ; *Halsophis leucomelas* D. and B. ; *Xenodon rhabdocephalus* Wied. ; *X. angustirostris* Peters ; *Lystrophis dorbignyi* D. and B. ; *Heterodon nasicus* B. and G. ; *H. platyrhinus* Latr. ; *Hypsirhynchus ferox* Gthr. ; *Uromacer oxyrhynchus* D. and B. ; *U. catesbyi* D. B. Right lung larger in *Uromacer*.

#### Scytalinae.

*Hydrocalamus quinquevittatus* D. and B. ; *Erythrolamprus venustissimus* L. ; *E. fissidens* Gthr. ; *Oxyrrhopus plumbeus* L. ; *O. fitzingerii* Jan. ; *Conophis pulcher* Cope ; *C. sumichrasti* Cope ; *Munolepis nasutus* Cope ; *Jaltris dorsalis* Gthr. ; *Philodryas viridissimus* L. ; *P. olfersii* Licht.

#### Natricinae.

Generally a proximal auricle or pocket. *Eutania proxima* Say ; *E. sirtalis* L., s. s. *sirtalis*, *obscura* and *parietalis* ; *Natrix fasciata* L. ; *N. rhombifera* Hallow. ; *N. taxispilota* Holbr.

#### Appendix to Colubridæ.

In the African *Thrasops flavigularis* Hallow. the right (rudimental) lung measures 5 mm. The trachea is enormously expanded transversely, simulating a tracheal lung, but its inferior wall contains the tracheal cartilages which extend its entire width, and it contains no cells or trabeculæ. An artery with lateral branches extends its entire length, which is from the posttracheal lung to the throat. This character distinguishes this genus from *Leptophis*.

In the following species I found no trace of the right lung.

Colubrinae. *Rhinoclitus lecontei* B. and G. ; *Cemophora coccinea* Blum. ; *Ophibolus doliatus* L. ; *O. getulus* L. ; *Pityophis melanoleucus* Daud.

Xenodontinae. *Halsophis angulifer* D. and B. ; *H. rudii* Cope.

Leptognathinæ. I propose this subfamily as distinct from the Xenodontinæ, on account of the presence of a large tracheal lung which is continuous with the normal lung, and with the trachea, and extends to the throat. *Leptognathus nebulatus* L.; *L. garmanii* Cope.

Scytalinæ. *Tachymenis strigatus* Gthr.; *Phalotris lemniscatus* D. and B.; *P. tricolor* D. and B.; *Erythrolamprus bipunctatus* Gthr.

Natricinæ. *Cerberus boæformis*; *Pseudaspis cana* L.

#### Acrochordidæ.

*Chersydrus granulatus* Merr. In this species the heart is at the middle of the length of the body, and the normal lung is posterior to it, extending nearly to the vent. No rudimental lung. A tracheal lung, composed of coarse cells and without lumen, extends from the heart to the head, and is discontinuous with the true lung. The trachea is closed, but communicates with the tracheal lung by a series of symmetrical pores on each sides

#### Najidæ.

One lung and a rudiment; no tracheal lung. *Pseudechis porphyriacus* Shaw; *Diemenia reticulata* Gray; *Naja tripudians* L.; *Bungarus semifasciatus* Kuhl.

#### Elapidæ.

No rudimental nor tracheal lung. *Elaps lemniscatus* L.; *E. fulvius* L.; *E. corallinus* L.; *E. multifasciatus* Jan.

#### Hydrophidæ.

I. One lung and no rudiment, continuous with tracheal lung, which extends to head.

*Hydrophis hardwickii* Gray (a slight constriction between tracheal and posttracheal lungs); *H. elliotii* Gthr.; *Hydrus bicolor* Daud.

II. A rudimental right lung connected with the left lung, which is separate from the large tracheal lung.

*Platurus laticaudatus* L.

### SOLENOGLYPHA.

A tracheal lung, continuous with the normal lung.

#### Causidæ.

No rudimental lung.

*Causus rhombeatus* Licht.

#### Dendraspididæ.

No rudimental lung.

*Dendraspis polylepis* Gthr.

*Viperidæ.*

No rudimental lung.

*Clotho arietans* L.

*Crotalidæ.*

I. No rudimental lung.

*Bothrops lanceolatus* L.; *Ancistrodon piscivorus* Lacep.; *Crotalophorus catenatus* Raf.; *Crotalus adamanteus* Beauv.; *C. confluentus* Say.

II. With a rudimental right lung.

*Bothrops pictus* Tsch.; *B. erythrorus* Cant.; *Teleuraspis schlegelii* Berth.; *Ancistrodon contortrix* L.; *Crotalus horridus* L.

### THE SYSTEMATIC VALUE OF THE PULMONARY CHARACTERS.

I have no doubt of the propriety of the separation of the Ungualliidæ from the other Peropoda, on account of its pulmonary characters. Nor is there any doubt in my mind of the necessity of the separation of the Leptognathinæ from the Xenodontinæ, for similar reasons. The genus *Heterodon* differs very much from the Xenodontinæ, in the possession of an enormous diverticulum of the lung, but as it is not present in the allied genus *Lystrophis* Cope, its wider distinction may be a questionable proceeding. The very marked characters of the genus *Chersydrus* characterize the family, as well as the osteological characters. It remains to be seen whether the family I termed the Nothopsidæ, but which Boulenger unites with the Chersydridæ, agrees with it in pulmonary characters. The remarkable tracheal lung or gland distinguishes the Epanodonta from the Catodonta, emphasizing that observed in the osteology of the skull. The peculiar form and relations of the maxillary bone in this group resemble those of the Solenoglypha, and there may be some possible connection between the groups. The tracheal body may be a degenerate tracheal lung, such as that division possesses.

The value of the rudimental right lung as a character of the Colubroidea is increased by my investigations. In only two genera have I found it present or absent, viz., *Halsophis* and *Pityophis*. I am not sure but that I may yet find it in the *P. melanoleucus*, where I have failed hitherto, but I am sure that it is present in some species of *Halsophis* and wanting in others. A natural group of American Colubrinæ, appears to be characterized by its absence, viz., *Rhinochilus*, *Cemophora* and *Ophibolus*; all genera with an entire anal shield. The development of cartilages in the bronchial foramen or tube of the rudimental lung is not a constant character. I found it in one *Heterodon platyrhinus* and not in another; it is present in *Conopsis pulcher*, but absent in *C. sumichrasti*.

The rudimental lung is often concealed from view and difficult to discover. The best test of its presence is the foramen which connects it with



the trachea, which will generally be found piercing the cartilage of the latter near the apex of the heart. The rudimental organ may then be found by inserting a bristle, and observing its destination through the more or less transparent tissues. In but one instance have I found a rudimental lung without a connecting foramen, viz., in the Mexican *Ficimia olivacea*. On the other hand, the foramen may terminate in a small blind sac.

The pulmonary characters may be determined without much dissection. The position of the heart must be first ascertained, and a longitudinal median incision made in the abdominal wall. In all forms except the Epanodonts and Catodonts, the trachea will be found passing to the left side of the heart, and entering the lung near its apex. By splitting the trachea, not too near its abdominal border, on turning the free margin upwards as the snake lies on its back, the *foramen bronchiale* will be seen and its lumen can be explored. The trachea is concealed by the œsophagus, which must be drawn to the left side of the body in order to make the examination. The examination of the tracheal lung requires the division of the abdominal wall further towards the head.

#### EXPLANATION OF PLATES.

The figures variously reduced ; the heart and liver are turned over to show the trachea and lungs.

##### PLATE XI.

*Typhlops liberiensis* Hallow.

##### PLATE XII.

*Charina bottæ* Blv.

##### PLATE XIII.

*Chersydrus granulatus* Merr.

##### PLATE XIV.

*Coluber quadrivittatus* Holbr.

##### PLATE XV.

*Heterodon platyrhinus* Latr.

##### PLATE XVI.

*Crotalus confluentus* Say.

#### LETTERING.

*Æ*, (Esophagus ; *St.*, Stomach ; *I.*, Intestine ; *R.*, Rectum ; *C.*, Cœcum ; *Tr.*, Trachea ; *R. L.*, Right lung ; *L. L.*, Left lung ; *T. L.*, Tracheal lung ; *B. F.*, Bronchial foramen ; *L.*, Liver ; *G.*, Gall bladder ; *K.*, Kidney ; *U.*, Ureter ; *T.*, Testis ; *V. D.*, Vas deferens ; *Ov.*, Ovary ; *Od.*, Oviduct ; *V.*, Vagina ; *F.*, Fontanelle ; *C. A.*, Corpus adiposum ; *H.*, Heart ; *A. R.*, Aorta root ; *Car.*, Carotid ; *J.*, Juglar vein ; *V. C.*, Vena cavi.